Acta Œcologica
Œcol. Gener., 1985, Vol. 6, n° 3, p. 243-260.

Arthropod overlapping recurrent groups in corticolous epiphytes: a case study

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ABSTRACT

This paper reports a study of the corticolous arthropod fauna living in epiphytic algae and lichens. Various recurrent groups have been defined using either the FAGER's procedure (REGROUP) or a new procedure forming overlapping groups (OVRGROUP). Two grouping criteria (FAGER's *vs.* KRYLOV's criteria) have also been tested. Groups defined both by either procedure and either criterion are discussed and compared from a biological and quantitative (occurrence, reliability) point of view. Recurrent groups or synusiae are related to the micro- (epiphyte) and macro- (phorophyte, site) habitats and to seasons. The biological meaning of the indicator species selected by the new algorithm is also investigated.

KEY-WORDS: *Recurrent groups - Association - Synusia - Corticolous fauna - Arthropods.*

RÉSUMÉ

La faune des arthropodes corticicoles vivant dans des algues et des lichens épiphytiques a été étudiée. Des groupes récurrents ont été déterminés en utilisant soit la procédure de FAGER (REGROUP), soit une nouvelle procédure menant à des groupes récurrents qui se chevauchent (OVRGROUP). Deux critères de groupement, celui de FAGER et celui de KRYLOV, ont également été testés. Les groupes obtenus à partir des 2 procédures et des 2 critères sont discutés et comparés d'un point de vue biologique et quantitatif (fréquence, fiabilité). Les groupes récurrents ou synusies sont liés aux micro- (épiphytes) et aux macro- (phorophytes, sites) habitats, ainsi qu'aux saisons. La signification biologique des espèces indicatrices sélectionnées par le nouvel algorithme est également discutée.

MOTS-CLÉS : *Groupes récurrents - Association - Synusie - Faune corticicole - Arthropodes.*

INTRODUCTION

There is a large amount of literature devoted to ecological groups. However, in spite of the high number of classification algorithms, few procedures have been specifically designed to identify such groups. This is clearly illustrated by LEGENDRE & LEGENDRE (1979) who comment numerous classification techniques but propose only two procedures to recognize what they call "biological associations".

One of these two procedures is that devised by FAGER (1957) and leads to the formation of "recurrent groups" *i. e.* groups of species which frequently occur

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Acta Œcologica/Œcologia Generalis, 0243-766X/85/03/243/18/$ 3.80/© Gauthier-Villars

together. This approach has been often utilized in oceanography to identify plankton groups (FAGER & MACGOWAN, 1963; SHEARD, 1965; KANAYA & KOIZUMI, 1966; KRYLOV, 1968; STONE, 1969; VENRICK, 1971; MACGOWAN & WALKER, 1979). It has also been used to recognize recurrent groups on the phytopsammon of a sandy beach (DAVIES, 1971), in salt marsh molluscs (MACDONALD, 1969), in demersal and fresh water fishes (FAGER & LONGHURST, 1968; LEGENDRE & BEAUVAIS, 1978) and in river macroinvertebrates (GHETTI & BONAZZI, 1977). The procedure has been applied to terrestrial Arthropoda in few cases, to the decaying oak wood fauna by FAGER (1968) and to litter and humus Oribatida by CROSSLEY & BOHNSACK (1960) and LEBRUN (1971).

As an extension of FAGER's procedure, a new algorithm has been proposed and described in detail in a previous paper (ANDRÉ, 1984 *a*). Briefly, this new algorithm is original in that it leads to the formation of overlapping recurrent groups, enables the identification of indicator species and avoids a bias intrinsic to FAGER's algorithm. However, the new algorithm needed supporting by a case study; this paper aims to provide such an opportunity and to illustrate how the algorithm behaves with complex data.

MATERIALS AND METHODS

Location of study sites

The study was carried out in Belgian Lorraine (southern Belgium), an area well known for its air purity and richness in corticolous lichens.

Three sites scattered over *ca* 5 km on the north slope of the Bathonian-Bajocian cuesta and located at the same altitude were visited (from east to west: Ruette, St-Mard *A* and St-Mard *B*; map in ANDRÉ, 1983).

Experimental design

Sampling was repeated quarterly during four seasons (from April 1973 to April 1974). For each season, 18 series of 25 samples were cut out from bark with pouches or merely brushed off. Samples constituting a series are characterized by the same phorophyte and epiphyte species and site. The complete list of the 18 series is detailed in ANDRÉ (1983, 1984 *b*, 1985). Surface area of crustose and foliose epiphyte samples did not exceed 25 cm². Consequently, the co-occurrence of two species in the same sample really means that they are close to each other.

As crustose, foliose and fruticose lichens were involved, sample processing included diverse techniques such as brushing, funnel extraction and smoking out depending on the phorophyte and the type of epiphyte (see ANDRÉ, 1984 *b*).

Data processing

Data consisted of four blocks of 18 series, one block per season. The real number of samples treated per season was 423 for spring, 414 for summer, 430 for autumn and 435 for winter (*). From a statistical point of view, this high number of samples minimized the bias denounced by HAYES (1978). The number of taxa considered per season turned around fifty. Recall that only binary (presence and absence) data are considered for the analyses below.

Data analysis

First, data were subjected to the FAGER procedure (REGROUP). Next, each block of 18 series was submitted to the new algorithm, OVRGROUP, using successively either FAGER's or KRYLOV's

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(*) The expected number of samples per season was 450 (18 × 25 samples). Due to different reasons (error, breaking, empty samples, etc.), the number of samples submitted to statistical analyses was slightly reduced.

grouping criterion (cf. André, 1984 *a*). Groups recognized by OVRGROUP whatever the grouping criterion selected will be called "strong forms" *sensu* Diday (1971).

Briefly, OVRGROUP is an iterative process based on the main rules:

1. A group includes the greatest possible number of interrelated species.

2. If several groups with the same number of species are possible, either Fager's or Krylov's criterion applies.

3. The number of species still to be classified after each iteration depends on the status of species belonging to the last group formed. Only "introverted" species, *i. e.* species having more links with species of its own group than with others, are removed from the pool of species to classify. This procedure, detailed in André (1984 *a*) and illustrated in appendix III, permits to avoid a bias intrinsic to Fager's algorithm (the first group comprises nearly always a real group plus some "ubiquitous" species which are no more associated with species of the first group than with others).

The method to select what species are interrelated is detailed in Fager (1957) and André (1984 *a*). In this particular case, the treshold value T computed from program AFFIN (*) was assessed separately for each block of data and set at a level corresponding to $p = 0.989$.

Grouping evaluation

Criteria are necessary to evaluate and compare grouping methods, specially to assess how much is a recurrent group peculiar to a given habitat. Four criteria will be used to characterize any group g: global frequency $G(g)$, local frequency $F(g)$, consistency $C(g)$ and independence $I(g)$:

$$G(g) = \frac{n(g)}{N}$$

$$F(g) = \frac{n(g, h)}{n(h)}$$

$$C(g) = \frac{n(g, h)}{n(g)}$$

$$I(g) = 1 - \frac{\displaystyle\sum_{i=1}^{X} \frac{n(g, i)}{n(g)}}{X - 1} \quad \forall i \neq g$$

where:

N is the total number of samples.
$n(h)$ is the number of samples collected in habitat h.
$n(g)$ is the number of samples containing group g.
$n(g, h)$ is the number of samples collected in habitat h, and containing group g.
$n(g, i)$ is the number of samples containing both groups g and i.
X is the number of recurrent groups determined by the algorithm.

Global frequency merely indicates how often a recurrent group has been observed whatever the habitat. In contrast, local frequency indicates whether a group is frequently found in a particular habitat. Unfortunately, both global and local frequencies are affected by the group size. Indeed, if species are distributed independently, the more species contains a group, the less frequent it is, and this makes difficult any comparison between groups of different size. However, this difficulty can be removed by comparing the observed frequency (G or F) to the expected frequency (ϕ) through the ratios ρ and τ:

$$\rho(g) = \frac{G(g)}{\phi(g)} \qquad \tau(g) = \frac{F(g)}{\phi(g)}$$

(*) Programs AFFIN, REGROUP and other related programs (CONNEX, STATION) are available from Dr. E. Venrick, Scripps Institution of Oceanography, La Jolla, CA 92093. OVRGROUP and a new version of CONNEX (dealing with overlapping groups) together with the user manual available from the author.

The expected frequency of a group g containing S species is:

$$\phi(g) = \prod_{j=1}^{S(g)} f(j)$$

where $f(j)$ is the observed frequency of species j in all the samples; and it postulates an independent distribution of species. The higher the ratios, the lower is the probability of finding a group at random either in general or in particular habitat.

Consistency is the degree to which a group is restricted to one habitat, *vs.* dispersed with more even occurrence in several habitats. This means that consistency informs about the reliability of a group as an indicator of a given habitat or, in other words, about its specificity to that habitat. When a group is euryecious, its local frequency and consistency are antagonistic. If the group habitat is defined vaguely, its consistency, $C(g)$, approaches the unit since $n(g, h)$ approaches $n(g)$ while its local frequency, $F(g)$, decreases since $n(h)$ increases; and conversely if the group habitat is defined more precisely.

Lastly, the independence criterion rests on the postulate that real synusiae are vicariant; accordingly, two synusiae should not be found in the same sample. A high value of $I(g)$ means that group g tends to be found alone in the samples and is independent of other groups.

RESULTS

As recurrent groups are composed of species living together, and thus observed at the same time, results will be analyzed season by season. Groups are illustrated by a set of 6 graphs (fig. 1 and 2). Species with their ID number are listed in appendix I and the biological interpretation of groups is given in appendix II.

Autumn recurrent groups (fig. 1, A-B)

Graphs in figure 1 show the affinities between species symbolized by a circled figure (*). Graph A displays the recurrent groups obtained by FAGER procedure while overlapping groups are illustrated in graph B. Comparison between both graphs prompts several comments:

1° FAGER'S algorithm distinguished 3 groups and 4 pairs of species whereas 8 groups and only 1 pair are recognized by the new algorithm. Among the 4 pairs distinguished by REGROUP, one *(171-34)* is also recognized by OVRGROUP (as a lateral branch), another *(31-12)* is disregarded and the last two, *(215-61)* and *(18-25)*, are encompassed in 3-species groups.

2° Overlapping groups allow the distinction of indicator (as *112*, *275*, *46*), component *(180, 47, 196)* and associate *(204)* species. The status of these species coincides very well with their biological distribution. For instance, the gamasid *Typhlodromus* cf. *tubifer (112)* peculiar to group A′, has an occurrence frequency of 68 % in the lichen *Parmelia sulcata* in Ruette (*i. e.* in the group habitat); its frequency is only 4.2 % in another foliose lichen growing in Ruette and drops down to 0 or 1 % in the other habitats. Constancy and fidelity of *T.* cf. *tubifer* for group A′ habitat are thus very high and justify its status of indicator species.

On the other hand, among the six most frequent species (*i. e.* caught in more than 100 samples), are found five component species, considered as ubiquitous or transition species *(Entomobrya nivalis (180)*, *Cerobasis guestfalicus (196)*, *Limothrips cerea-*

(*) Autumn data processing and group forming procedure are detailed in appendix III.

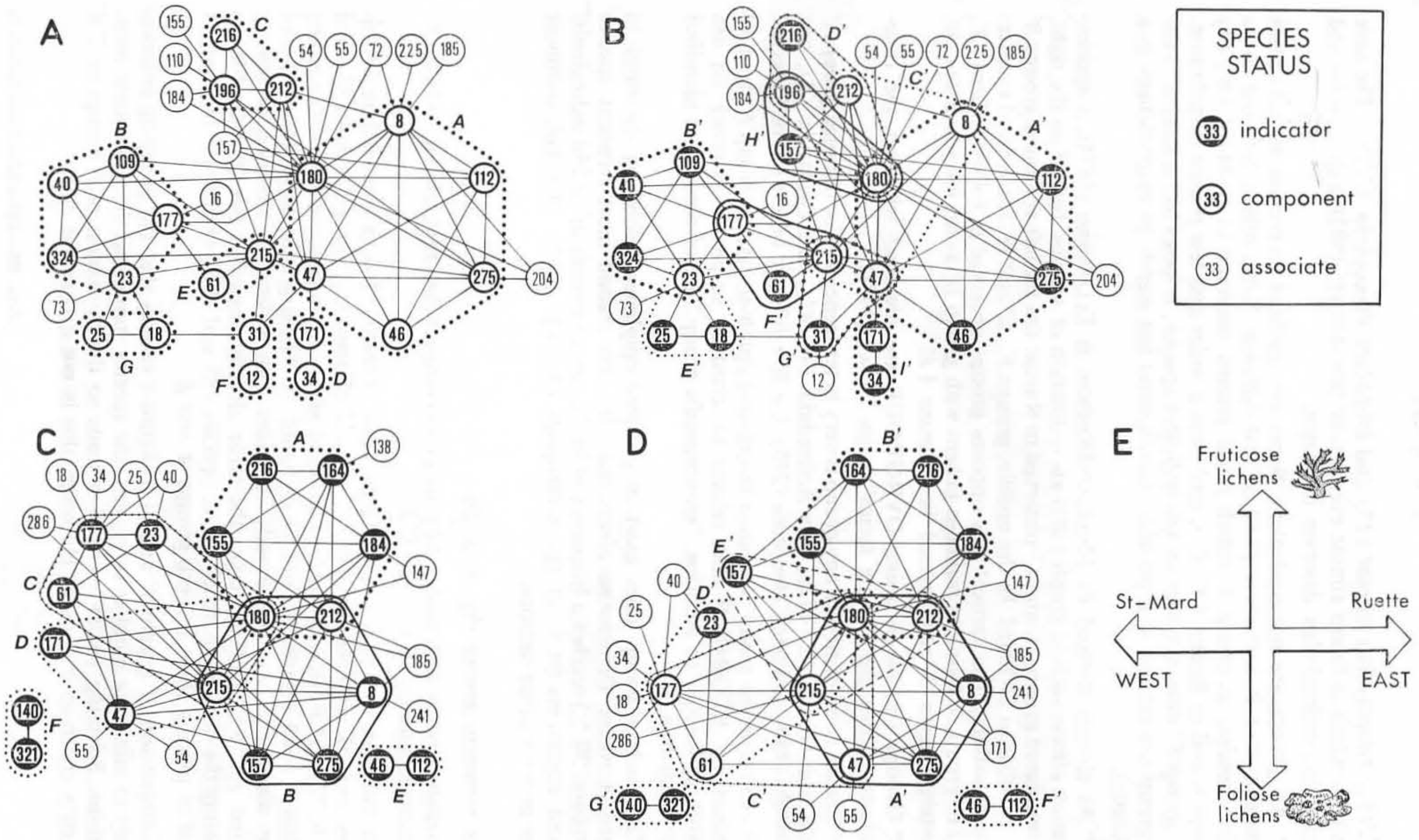

FIG. 1. — Graphs illustrating the affinities between species in autumn (*A*, *B*) and winter (*C*, *D*), with the corresponding diagrammatic interpretation (*E*). *A*: groups formed by REGROUP; *B-D*: overlapping recurrent groups determined by using either FAGER's (*B*, *D*) or KRYLOV's (*C*) criterion.

lium (215), *Triophtydeus lebruni (47)* and immature Psocoptera *(212))*. The case of *E. nivalis* which is found almost everywhere (see ANDRÉ, 1983) is descriptive and obviously this collembolan deserves its status.

3° All groups are not equivalent. Some are confined to precise microhabitats as groups *A'* and *B'* and correspond to real synusiae. Some others turn out to be transition groups, as group *F'* which joints groups observed in St-Mard *(B', E')* to groups found in Ruette *(A', C')*, and have a wider and less precise distribution. Lastly, group *C'* does not contain any indicator species; it looks like a kind of "residual" group not related to a peculiar microhabitat but merely to macrolichens in a site (Ruette).

4° As already noticed by MUELLER-DOMBOIS & ELLENBERG (1974), a species-association plexus such as graph 1 *B* is an ordination of species. Indeed on the right, are encountered groups *A'* and *C'* observed in Ruette. On the left are found groups *B'* and *E'* peculiar to St-Mard. In the middle, groups *F'*, *G'* and *H'* correspond to intermediate situations. The vertical axis opposes groups observed in foliose lichens (*A'*, *B'*, *F')* to group *D'* found in fruticose lichens with group *H'* as an intermediate case. This interpretation is summarized in diagram 1 *E*.

5° Groups formed by using OVRGROUP are identical whatever the criterion selected. They are "strong forms" *sensu* DIDAY (1971).

6° Species composition of any group is very heterogeneous. For instance, group *A'* contains one Gamasida *(112)*, two Actinedida *(46, 47)*, one Oribatida *(8)*, one Collembola *(180)* and one Coleoptera *(275)*, *i. e.* five different orders out of 6 species.

7° No recurrent group is peculiar to crustose epiphytes except group *F* (fig. 1 *A*) recognized by REGROUP and related to crustose epiphytes growing on ash and birch in Ruette. In addition, "monospecific groups" are of course not identified by any algorithm.

Yet, such a group does exist in crustose epiphytes colonizing chestnuts in St-Mard *A* where *Dometorina plantivaga (31)*, the second most frequent species (occurrence: 39 %) reaches a frequency of 96 %, a mean density of *ca* 250 individuals/dm^2 and represents 88 % of the arthropods (ANDRÉ, 1985). This last comment applies also to other seasons.

Winter recurrent groups (fig. 1, *C-D*)

Graphs dealing with winter data are more compact than that relating to autumn; their connectance is 34.5 % *vs.* 27.8 %.

In addition to two pairs, *(112-46)* and *(321-40)*, FAGER's procedure distinguishes only 3 recurrent groups *(8-275-212-47-180-215)*, *(184-216-164-155)* and *(61-23-177)*. OVRGROUP lead to different groupings depending on what grouping criterion is used (graphs *C* and *D* in figure 1). These graphs show two 6-species groups which overlap. This exactly coincides with a fictitious situation previously analyzed and REGROUP makes the error already described (see ANDRÉ, 1984 *a*) by putting the ubiquitous species (*i. e.* species *180* and *212*) exclusively in group *A* instead of placing them in both groups *A* and *B*.

Comparison of graphs *C* and *D* in figure 1 reveals that the grouping criterion is likely to affect the number of groups, the species status and the subsequent interpretations. Selecting FAGER's criterion leads to the formation of 6 groups *vs.* 7 if KRYLOV's criterion is chosen. However, this is not a constant rule.

Species status is also affected by the grouping criterion. Groups *B* and *A'* in graphs *C* and *D* in figure 1 contain the same species but one and are thus analogous. In graph *C* (KRYLOV criterion), *Moebilia penicillata (157)* is included in group *A* whereas *Triophtydeus lebruni (47)* takes its place in graph *D* (FAGER criterion). It results that *T. lebruni (47)* appears to be either an indicator species (graph *C*) or a component one (graph *D*). Now, this actinedid mite is very frequent in winter (present in 44 % of samples) and even the most frequent arthropod in summer (34 %) and spring (46 %). Consequently, the status of ubiquitous component species seems much more adequate to characterize this mite.

Besides, even if analogous groups *A'* and *B* are very similar in their composition, they differ in their biological interpretation. While group *A'* is observed in the 3 series of foliose lichens sampled in Ruette, and only in those 3 series, group *B* is found in only two of them, *i. e.* in *P. sulcata* on poplar and in *P. acetabulum* on ash, but not in *P. sulcata* on ash. Distribution of group *B* turns out to be difficult to explain and proves to be less cogent than that of group *A'*. Accordingly, FAGER's criterion is preferred to that proposed by KRYLOV.

Lastly, the ordination summarized in diagram 1 *E* also applies to graph 1 *D*.

Spring recurrent groups (fig. 2 *A*)

FAGER's program REGROUP distinguishes only two recurrent groups (groups *A* and *C* in figure 2 *A*) plus two pairs *(25-18)* and *(23-177)*.

Figure 2 *A* illustrates the groups formed by OVRGROUP when KRYLOV's criterion is selected. Using FAGER's criterion leads to the same grouping plus three other groups, *(215-47-180-8-171)*, *(31-215-47)* and *(34-171-47)*. Groups illustrated in figure 2 *A* and detailed in appendix II are thus strong forms. Despite a weak connectance (27.8 %), groups are less individualized than with autumn data, their interpretation is less precise and they are less independent.

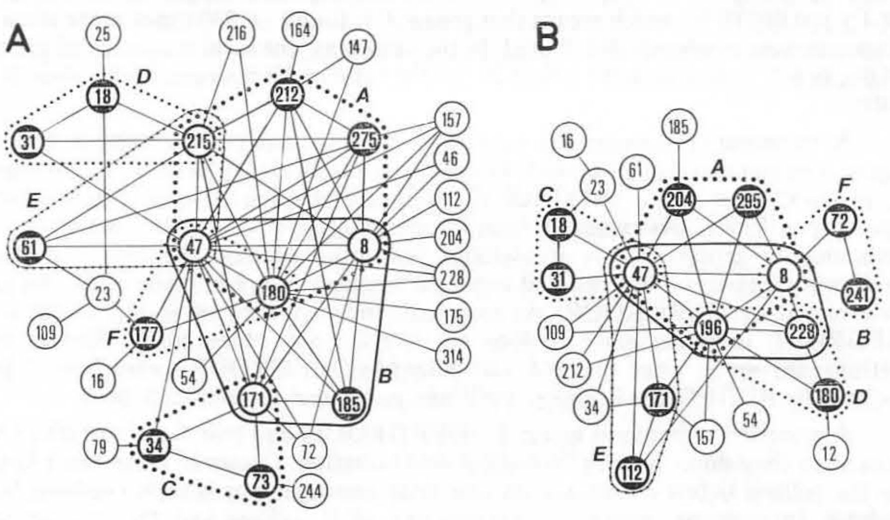

FIG. 2. — Graphs illustrating the affinities between species in spring (*A*) and summer (*B*). Only strong forms recognized by OVRGROUP are outlined.

Summer recurrent groups (fig. 2 *B*)

Graph *B* of figure 2 reveals the weak number of inter-specific links. The program REGROUP recognizes only group *A* plus four pairs of species *(23-18)*, *(34-171)*, *(180-12)* and *(72-241)*. Figure 2 *B* illustrates only strong forms determined by OVRGROUP and detailed in appendix.

General comments made about the spring data are still approximate: groups are vaguely defined with a weak independence. The summer drought seems to desorganize completely the interspecific relationship network, especially in St-Mard where only one recurrent group has been recognized. The contrast between Ruette where a few groups subsist and St-Mard could be explained by their respective situation: Ruette is a kind of very small wood where the microclimate should be milder than in St-Mard stations constituted of trees planted along roads.

DISCUSSION

This section will be twofold as it aims to highlight both the algorithm properties (*i. e.* technical aspects), and the biological meaning and properties of recurrent groups (*i. e.* conceptual aspects) as revealed by the study of corticolous arthropods.

Overlapping vs. *exclusive groups*

Autumn species groupings illustrated by the plexus diagrams of figure 1 offer a descriptive example of the differences between both algorithms. The mean global frequency of groups distinguished by REGROUP is somewhat greater than that of groups defined by OVRGROUP (39 *vs.* 27 %). However, as outlined previously, the frequency of a group depends on its size. In this case, the respective mean sizes are 3.14 *vs.* 3.78 species.

Local frequencies of overlapping groups may appear to be low at first sight. That of group *A'* is only 2 %. However, the expected frequency of this group, $\phi(A')$, is 0.00215 %, which means that group *A'* is found *ca* 930 times more often than if species were randomly distributed. In the same way, the local frequency of group *B'*, $F(B')$, is 8 % whereas $\phi(B')$ is 0.0125 %; the ratio $\tau(B')$ between both values is thus 640!

A quantitative comparison between analogous groups in graphs *A* and *B* on figure 1 is summarized in table I. Group *D'* in graph *B* (OVRGROUP) corresponds to group *C* in graph *A* (REGROUP); both are characteristic of fruticose lichens, specially in Ruette. As expected, local frequency of group *D'*, $F(D')$, is slightly lower than that of group *C* since it includes one more species. However, consistency, and ratios between observed and expected frequencies are in favor of *D'*, the group determined by OVRGROUP. As expected, independence of group *C* defined by REGROUP is higher since it does not overlap any other group. Similar observations are made when group *F'* recognized by OVRGROUP is compared to pair *E* isolated by REGROUP. Roughly, both are particular to foliose lichens.

A comparison between group *E'* (OVRGROUP) and pair *G* (REGROUP) is less cogent as they differ in their biological interpretation. Group *E'* is the most frequent in the foliose lichen *P. sulcata* on chestnut although not strictly confined to this habitat. In contrast, pair *G* is characteristic of *P. sulcata* and *Protococcus viridis*, the two epiphytes collected on chestnut. If pair *G* was supposed to be characteristic of *P. sulcata* on chestnut as group *E'*, its consistency would drop down to 38 % with an identical local frequency. On the other hand, the ratio $\tau(E')$ is much higher than $\tau(G)$: 139 *vs.* 21. This example shows nevertheless that both algorithms lead to different interpretations: OVRGROUP would tend to isolate groups of well-defined habitat even if they are not strictly confined to them.

TABLE I. — *Quantitative comparison between three pairs of analogous groups recognized either by REGROUP or OVRGROUP.*

	GROUP C (1)	GROUP D' (2)	GROUP G (1)	GROUP E' (2)	GROUP E (1)	GROUP F' (2)
Number of species, S	3	4	2	3	2	3
Global frequency, G	4.19 %	3.49 %	3.02 %	1.86 %	6.74 %	2.79 %
Local frequency, F	20.00 %	17.33 %	18.37 %	20.83 %	13.50 %	9.60 %
Consistency, C	83.33 %	86.67 %	69.23 %	62.50 %	93.10 %	100.00 %
Independance, I	99.07 %	90.00 %	96.15 %	98.44 %	95.98 %	93.75 %
Expected frequency, Φ	1.36 %	0.56 %	0.66 %	0.15 %	4.60 %	0.98 %
Ratio G/Φ, ρ	3.07	6.25	3.50	12.40	1.47	2.83
Ratio F/Φ, τ	14.67	31.07	21.36	138.89	2.93	9.75

(1) Group defined by REGROUP.
(2) Group defined by OVRGROUP.

FAGER'S vs. KRYLOV'S *grouping criterion*

Winter species groupings illustrated in figures 1 *C* and *D* offer a descriptive example of the respective effects of both criteria. As already outlined in the previous section, the grouping obtained by using FAGER'S criterion presents advantages as for the species status and the biological interpretation of groups. A quantitative comparison is presented in table II, where only groups restricted to either grouping are selected.

TABLE II. — *Quantitative comparison between groups defined by OVRGROUP using either* FAGER'S *or* KRYLOV *criterion.*

	Krylov's criterion		Fager's criterion		
	GROUPS		GROUPS		
	B	D	A'	C'	E'
Number of species, S	6	4	6	5	4
Global frequency, G	0.69 %	4.14 %	2.76 %	2.30 %	4.14 %
Local frequency, F	4.00 %	22.67 %	16.00 %	13.33 %	22.67 %
Consistency, C	100.00 %	94.44 %	100.00 %	100.00 %	94.44 %
Independance, I	100.00 %	96.67 %	95.83 %	88.33 %	95.37 %
Expected frequency, Φ	0.04 %	1.14 %	0.11 %	0.66 %	0.83 %
Ratio G/Φ, ρ	18.11	3.62	25.41	3.47	4.96
Ratio F/Φ, τ	105.03	20.98	147.37	20.20	27.15

It turns out that groups formed by using FAGER's criterion are both more frequent and less "expected" than those formed by selecting KRYLOV's criterion. Actually, this is not really surprising since FAGER's criterion tends to maximize the sum of interspecific affinities of groups it selects. On the other hand, groups formed by using KRYLOV's criterion have a greater independence. This is not surprising either since KRYLOV's criterion tends to form groups with a minimum of links with outer species. Nevertheless, group *B* which is very similar in its composition to group *A'*, is four times rarer and looks like a "mathematical artifact".

Resonance

The resonance (*) phenomenon is well illustrated by groups *C'* and *D'* in figure 1 *D:* they overlap so much that four species out of five are common to both groups. Their respective interpretation are very similar: both are found in large foliose lichens on poplar in St-Mard *B*, and occasionally in *P. sulcata* in St-Mard *A*. Their relative independence is low: 40 % of samples which contains either one group contains also the other. Everything happens "as if the algorithm did not know which group to select". Either species *47* or *23* may joint indifferently the four common species *(215-180-61-177);* both groups are said to be in resonance.

Such a phenomenon could be interpreted as the result of a missing link. Indeed, one more link, and only one, between species *47* and *23* would have been necessary to get a third 6-species group *(47-215-180-61-177-23)*. This "potential" 6-species group has the same habitat as group *C'* with a local frequency of 8 %, a consistency of 100 %, and a ratio τ of 73. This explains the strong similarity observed between groups *C'* and *D'* and suggest the need for additional data.

In such a case, either group can be selected, knowing they are very close to each other. Another solution would consist in favoring a strong form, in this case, group *D'* which corresponds to group *C* selected by using KRYLOV criterion (fig. 1 *C*).

Arthropod recurrent groups as synusiae

First of all, it must be recalled that recurrent groups are composed of species occurring frequently together (for a formal definition, see ANDRÉ, 1984 *a*). In this study, the frequent co-occurrence of the component species forming a recurrent group has been observed and quantified. As a result, a recurrent group is a *real* unit and should not be confused with any community-type which, as a class concept, is inescapably an abstraction (WHITTAKER, 1973). Recurrent groups are thus essentially different from "classes" defined through traditional-cluster analyses or derived from ordination techniques.

As noted above, all the recurrent groups are not equivalent. Some are confined to well-defined microhabitats while others are peculiar to a site irrespective of the epiphyte and phorophyte species. As a result, the habitat of a latter group may encompass that of a former group (see, for instance, habitats of groups *A'* and *C'* in autumn). Microhabitat-type groups *vs.* large habitat groups do not however constitute a hierarchical system similar to that used in vegetation classification. They merely coincide to different resolution levels or scales. At a large scale, corticolous biota may be perceived as being homogeneous (see GILBERT, 1971) and characterized

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(*) By analogy with the phenomenon of interrelated alternative bond structures observed in certain molecules and called resonance in chemistry.

by a set of euryecious species; at a finer scale, however, it becomes definitely heterogeneous and appears to be composed of various units related to microhabitats (André, 1985).

Corticolous arthropod recurrent groups defined in terms of co-occurrence of their component species, and characterized by a peculiar habitat, most often a microhabitat, accord with the concept of synusia defended by Mueller-Dombois & Ellenberg (1974). They also approximate the concept of "ecological groups" as defined by Duvigneaud (1946, 1980) who stresses the ecosociological affinities. In addition, recurrent groups confined to well-defined microhabitats appear to be elementary units associated with an "ecological niche" and answer the concept of synusia proposed by Lebrun (1961). If the seasonal pattern (temporal separation) is taken into account in addition to the spatial separation above-mentioned, the arthropods recurrent groups parallel the concept of synusia (*) advanced by Barkmann (1973).

As noted by Mueller-Dombois & Ellenberg (1974), a synusia may be composed of quite unrelated species. This is precisely the case of corticolous recurrent groups which are highly heterogeneous from a systematic point of view. Their definition would have been impossible if the study had been focused on a single arthropod order.

Seasonal pattern

Despite their association with a permanent habitat, the corticolous recurrent groups vary greatly from one season to another.

Quantitatively, the group mean size is 3.78, 4.29, 3.83 and 3.38 species from autumn to summer. The mean number of affinities per species varies in the same way (successively 2.60, 2.63, 2.34 and 1.43 from autumn to summer). These figures highlight a collapse of the affinity network during the summer period.

On the other hand, if figures 1 *B*, 1 *D*, 2 *A* and 2 *B* are analyzed comparatively, it is difficult to find out a group common to the four seasons. At the very most, some "associations" are recurrent throughout the year, such as *(180-47-8)*. This is explained, in part, by the seasonal occurrence of numerous species (phloiophilous *vs.* phloiobiontic species, cf. André, 1983). For instance, Psychodidae *(295)* are observed only in summer while the collembolan *Vertagopus arborea (177)* is a winter species (André, 1983). In addition, even if some species are found during the four seasons, their relative position and their affinities vary from one graph to another. This expresses structural variations of the affinity network, which superimposes onto the seasonal composition variations (migrations of phloiophilous species), and emphasizes the temporal meaning of recurrent groups conceived as synusiae.

Meaning of the species status

Some confusion revolves around the different interpretations placed upon what is called a "character-species" or an indicator species in ecology. This compels the meaning of indicator species in a recurrent group to be clarified. This first point to stress is the definition given previously: indicator species are those which belong to only one group and, usually, are introverted (*i. e.* have more links with species of their own group than with others) (see André, 1984 *a*). This definition does not mean that the

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(*) Actually, the recurrent groups conceived as real units correspond to the "societies" of Barkmann (1973) whose equivalent abstract units are the synusiae.

affinity values (α-values) are higher between indicator species than between others. But it results in τ-values higher between indicator than between mere component species. For instance, the mean τ-value between indicator species of autumn group A' is 4.10 ± 1.86 *vs.* 1.71 ± 0.31 between the other components. This clearly means that the co-occurrence of indicator species is less expected than that of others—which actually is not surprising since others are transition, euryecious or ubiquitous, species—and accordingly more significative.

Does the above definition imply that an indicator species be constant and/or has fidelity for its group? To answer this question, suppose that autumn group A' is found whenever at least four of its component species co-occur in a sample. Defined in this manner, group A' was found 19 times, nearly always in foliose lichens on ash in Ruette (its local frequency reaches 38 % with a consistency of 95 %). Fidelity and constancy of the component species are shown in table III; these values do not allow any discrimination between indicator and more component species.

TABLE III. — *Constancy and fidelity of group A′ species in autumn.*

Species (ID No.)	Status	Constancy[1]	Fidelity[2]
E. nivalis (180)	component	100.0	2.3
T. lebruni (47)	component	89.5	5.0
E. oblongus (8)	component	73.7	13.6
T. cf. *tubifer* (112)	indicator	94.7	13.5
O. fagi (275)	indicator	94.7	6.3
P. vegei (46)	indicator	68.4	30.3

(1) Constancy: number of samples containing group A' and the component species/number of samples containing group A'.

(2) Fidelity: number of samples containing group A' and the component species/number of samples containing that species.

All values expressed in percent.

On the other hand, recurrent groups have been related to particular habitats. Would the indicator species be indicators of these habitats? A quantitative comparison si offered in table IV which shows the constancy and fidelity of different species to group-habitats (and not to groups themselves) in autumn. From the analysis of table IV, it turns out that:

— component species have a better score "constancy-fidelity" for their own group habitat than for any other;

— the score reached by an associate species (see species *204*) is lower than those of component species;

— the mere component species display high values of constancy-fidelity in the habitats of the various groups which they belong to;

— generally, the indicator species have by far the highest score in their own group habitat; of course, if a species characterizes a microhabitat type group, its fidelity is higher for a large habitat which encompasses that microhabitat (compare fidelity of species *112*, *275*, and *46* in group *A'* and *C'* habitats); however, there may be striking exceptions as for instance *O. fagi (275)* which have a 50 % constancy in *Parmelia sulcata* on chestnut in Ruette, which is quite different from group *A'* habitat.

TABLE IV. — *Constancy and fidelity of some species for the habitat of various groups in autumn.*

	Habitat of groups																				
	A'			B'			C'			D'			E'			F'			G'		
	St.	Co.	Fi.	St.	Co.	Fi.	St.	Co.	Fi.	St.	Co.	Fi.	St.	Co.	Fi.	St.	Co.	Fi.	St.	Co.	Fi.
T. cf. tubifer (112)	I	68	92	-	1	3	-	28	95	-	0	0	-	0	0	-	16	54	-	28	95
O. fagi (275)	I	58	36	-	15	19	-	39	60	-	15	14	-	50	15	-	24	38	-	47	73
P. vegei (46)	I	50	76	-	1	1	-	23	88	-	0	0	-	0	0	-	10	39	-	24	91
E. oblongus (8)	C	52	40	-	3	5	C	46	88	-	19	22	-	13	5	-	12	23	-	40	75
E. nivalis (180)	C	82	24	-	30	17	C	76	54	C	83	26	-	13	2	-	42	31	-	49	35
T. lebruni (47)	C	68	28	-	32	27	C	47	48	-	27	17	-	13	3	-	41	43	C	54	56
P. fusciceps (204)	A	22	38	-	0	0	A	23	97	-	0	0	-	0	0	-	9	38	-	23	97
T. richteri (109)	-	10	11	I	45	49	-	15	20	-	19	15	-	13	3	-	38	51	-	27	36
Eupodes sp. (40)	-	10	10	I	30	56	-	6	15	-	16	23	-	4	2	-	28	67	-	10	23
Isopoda (324)	-	0	0	I	46	61	-	1	2	-	13	18	-	0	0	-	37	81	-	8	18
V. arborea (177)	-	12	7	C	77	84	-	11	15	-	12	10	-	0	0	C	65	88	-	14	18
T. trimaculatus (23)	-	0	0	C	52	71	-	0	0	-	12	12	C	50	16	-	42	71	-	18	16
D. degeeri (216)	-	4	2	-	2	2	-	24	37	I	45	42	-	21	6	-	2	4	-	11	17
Psocoptera im. (212)	-	46	45	-	4	4	I	60	73	I	53	40	-	21	5	-	13	16	-	36	44

St.: status; Co.: constancy; Fi.: fidelity; im.: immatures; I: indicator species; C: component species; A: associate species; wavily underlined items indicate species scores in their own group habitat; underlined figures refer to outliers.

All values expressed in percent.

In conclusions, all component species in a recurrent group are rather constant and have fidelity for their group but indicator species differ from mere components by their single membership, their usual introversion toward species of their own group and their unexpected co-occurrence. Besides, indicator species are likely to be indicators of their group microhabitat.

CONCLUSIONS

From a practical point of view, the new algorithm OVRGROUP proves to be applicable to field data. In the case study presented above, 61 species *X* 400 relevé matrices were handled with no problem.

From a biological point of view, the new procedure has made it possible to define recurrent groups which are coherent and ecologically meaningful. In particular, recurrent groups turn out to be synusiae related to habitats and seasons, *i. e.* real units to which concrete values (occurrence frequency, etc.) may be associated. Besides, the new algorithm avoids a bias intrinsic to FAGER's algorithm and enables the identification of indicator species, which helps in the biological interpretation of groups.

Lastly, the procedure is based on species frequency values and appears to be a powerful analysis tool wherever densities or abundances are difficult to assess (field censuses, trapping, oceanography, etc.).

ACKNOWLEDGEMENTS

My sincere thanks are due to Dr. Ph. Lebrun under whom this work was achieved and to Drs. E. L. Venrick (La Jolla, CA) and J. A. Wallwork (London, U. K.) for reading and criticizing the manuscript. I am also grateful to Dr. Venrick for providing the set of programs dealing with recurrent groups.

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APPENDIX I. — List of the taxa with their *ID* number.

ORIBATIDA (ACARI)

8	*Eueremaeus oblongus*
12	*Carabodes labyrinthicus*
16	*Tectocepheus sarekensis*
18	*Cymbaeremaeus cymba*
23	*Trichoribates trimaculatus*
25	*Humerobates rostrolamellatus*
31	*Dometorina plantivaga*
34	*Phauloppia lucorum*

ACTINEDIDA (ACARI)

40	*Eupodes* sp. *A*
46	*Pseudotriophtydeus vegei*
47	*Triophtydeus lebruni*
54	*Tydeus bedfordiensis*
55	*Tydeus stefani*
61	*Homeotydeus formosa*
72	*Cunaxa* sp.
73	*Cunaxoides* sp.
79	*Mediolata mariaefrancae*

GAMASIDA (ACARI)

109	*Typhlodromus richteri*
110	*Typhlodromus foenilis*
112	*Typhlodromus* cf. *tubifer*

ARANEIDA

138	Undetermined immatures
140	*Lathys humilis*
147	Immature Thomisiidae
155	Immature Theridiidae
157	*Moebilia penicillata*
164	Immature Linyphiidae

COLLEMBOLA

171	*Xenylla brevisimilis*
175	*Anurophorus laricis*
177	*Vertagopus arborea*
180	*Entomobrya nivalis*
184	*Orchesella cincta*
185	*Willowsia platani*

PSOCOPTERA

196	*Cerobasis guestfalicus*
204	*Pseudopsocus fusciceps*
212	Undetermined immatures

THYSANOPTERA

215	*Limothrips cerealium*
216	*Dendrothrips degeeri*

HETERO- & HOMOPTERA

225	Anthocoridae (sp. *A*)
228	*Loricula elegantula*
241	*Pseudochermes fraxini*

OTHER INSECTS

244	*Raphidia* larvae
275	*Orchestes fagi* (Coleo-)
286	Melyridae larvae
295	Psychodidae
314	Chalcidoidea

DIPLOPODA

321	*Polyxenus lagurus*

CRUSTACEA

324	Undetermined Isopoda

APPENDIX II. — List of overlapping recurrent groups for each season.

Each group is characterized by its habitat, local frequency (*F*), consistency (*C*) and independence (*I*).

	F(*)	*C*	*I*
Autumn (fig. 1 *B*)			
A' foliose lichens on ash in Ruette	2-24	100	94
B' foliose lichens on poplar in St-Mard *A* and *B*	8-10	100	94
C' foliose and fruticose lichens in Ruette	8	100	88
D' fruticose lichens in Ruette, and secondarily in St-Mard *A*	17	97	90
E' most often in *Parmelia sulcata* on chestnut in St-Mard *A*	21	93	98
F' foliose lichens on poplar in St-Mard *A* and in *P. sulcata* on ash in Ruette	10	100	94
G' foliose lichens on poplar and ash in Ruette and St-Mard *A*	10	91	93
H' fruticose lichens in Ruette and St-Mard *A* and in *P. sulcata* in Ruette	18	96	94
I' foliose and fruticose lichens in poplar in St-Mard *A*	32	94	97
Winter (fig. 1 *D*)			
A' foliose lichens on ash and poplar in Ruette	16	100	96
B' fruticose lichens on ash in Ruette	16-58	100	96
C' large foliose lichens on poplar in St-Mard *B*, occasionally in *P. sulcata* on chestnut in St-Mard *A*	13	100	88
D' large foliose lichens on poplar in St-Mard *B*, occasionally in *P. sulcata* in St-Mard *A*	11	100	88
E' in *P. sulcata* and *Evernia prunastri* on ash and in *P. acetabulum* on poplar in Ruette	23	94	94
F' foliose lichens in Ruette, mainly on ash	16	92	97
G' in *P. sulcata* on chestnut in St-Mard *A*	24	100	92
Spring (fig. 2 *A*)			
A in *P. sulcata*	9	100	82
B foliose lichens in Ruette	15	100	89
C in *P. sulcata* in St-Mard *A*	38	100	82
D crustose and foliose epiphytes in St-Mard *A*, in *Lecanora conizaeoides* on birch in Ruette	12	100	92
E in *P. sulcata* and *P. acetabulum* on poplar and chestnut in St-Mard and on ash in Ruette	17	95	90
F in all foliose lichens (except in *P. acetabulum* on ash in Ruette) + *E. prunastri* on poplar in St-Mard *A*	13	96	94
Summer (fig. 2 *B*)			
A foliose lichens in Ruette	8	86	94
B in *P. sulcata* in Ruette	8	100	75
C in crustose epiphytes on chestnut in St-Mard *A* and in *P. sulcata* in Ruette and St-Mard *A* (except on chestnut)	11	100	99
D foliose lichens in Ruette, occasionally in fruticose lichens	7	100	92
E foliose lichens on ash in Ruette	14	100	83
F foliose lichens on ash in Ruette	8	100	90

(*) A second frequency value indicates the co-occurrence frequency of indicator species as a whole. All values expressed in percent.

APPENDIX III

This appendix details the first four steps of OVRGROUP procedure applied to autumn data, using FAGER's criterion (fig. 1 *B*).

The first step consists in forming group *A′* with 6 species. Species *275*, *112* and *46* are introverted and thus considered to be indicator species, accordingly they are removed from the set of species to classify. In contrast, species *180*, *8* and *47* are extroverted and maintained in the pool of species to classify until the end of the procedure; as a result, they are likely to belong to other groups. Six species are associated with group *A′*: *54, 55, 72, 185, 204, 225*.

At the second step, three 5-species groups are found; group *B′* with species *23, 177, 109, 40* and *324* is selected because its species have the largest total of affinities (FAGER's criterion). Species *40*, *109* and *324* are introverted, considered as indicator species and also removed from the set of species still to classify while species *23* and *177* are extroverted and maintained in that set. Species *16* and *73* are associated to group *B′*.

The third step consists in forming group *C′* with four extroverted species *(180, 215, 47, 8)* and only one introverted *(212)*. As the latter species is linked only to extroverted species, *i. e.* to euryecious or ubiquitous species, it is not considered to be an indicator species at this step and it remains in the set of species to classify until it belongs to another group (see rule 3 in ANDRÉ, 1984 *a*). The status of species *8*, *47* and *180* is fixed since they belong already to group *A′* while the status of species *215* is shelved.

At the fourth step, group *D′* is selected among seven 4-species groups. Species *216* is introverted, considered as an indicator species and removed from the set of species to classify. Species *212* is also removed from this set since it was a single introverted species at step 3; it will be not considered as an indicator species since it belongs now to groups *C′* and *D′*. Species *180*, a typical ubiquitous species, belongs now to three groups. Species *196*, which is extroverted, is also maintained in the set of species to classify until the end of the procedure.